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Recent Studies on Flavor Aversion Learning in Wildlife Damage Management

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ABSTRACT

Flavor aversion learning (FAL) occurs experimentally when a mammal is presented with a distinctive-flavored food followed by a postingestional illness. Birds may learn aversions to visual cues. Aversions follow a single pairing and may be robust. During the past decade, at least four directions were followed in evaluating FAL for managing wildlife damage: compounds already registered for use on crops such as herbicides, insecticides, or fungicides were tested for their abilities to also repel birds and small mammals from crops; naturally occurring compounds such as sucrose or charcoal were similarly evaluated; eggs were treated with different compounds in attempts to protect untreated eggs from predators; and FAL was used as a model for understanding bait shyness associated with some rodenticides. Use of registered pesticides, or naturally occurring and generally regarded as safe ones, reduces costs for registration, but also limits choices of potential repellents. No mammalian or avian repellents based on FAL are presently registered. Most research is based on a single model of FAL in which the flavor (or visual cue) is paired within 6 hours with postingestional illness, and that flavor or similar flavors (through generalization) are subsequently avoided. Other models of FAL, including those based on overshadowing and salience rather than generalization of learned aversions, might offer applications.

KEY WORDS

bait shyness, damage, flavor aversion learning, management, overshadowing, repellents, salience, wildlife

INTRODUCTION

Flavor aversion learning (FAL) occurs experimentally when a mammal is presented with a distinctive-flavored food (conditioned stimulus) followed by an illness-inducing agent (unconditioned stimulus). Birds may learn aversions to visual cues (e.g., Mason and Reidinger 1983*b*). Aversions occur after a single pairing of stimuli, can be robust, and generalize to similar flavors or visual cues. These attributes have stimulated interest in possible applications of FAL to managing wildlife damage (Figure 1).

Scientific literature on FAL and its attributes as it relates to specific aspects of wildlife damage management has already been reviewed and summarized (e.g., Dorrance and Gilbert 1977, Rogers 1978*a*, Reidinger and Mason 1983, Gustavson and Gustavson 1985, Prakash 1989, Maizeret 1993). In this paper, I illustrate recent directions, mostly since 1983, in research on applications of FAL to wildlife damage management and then suggest some directions that warrant further attention.

RECENT DIRECTIONS IN RESEARCH

Firstly, there is a body of recent literature by scientists who use FAL to further understand bait shyness to baits containing rodenticides and other vertebrate pesticides. Secondly, some scientists focus on the registration or reregistration of wildlife management pesticides. Thirdly, scientists try to find compounds already registered as pesticides, or that occur naturally and are generally regarded as safe, which also function as effective vertebrate repellents. Costs would presumably be relatively low for the registration of such repellents. Fourthly, some scientists have explored using FAL to reduce predation on wildlife, particularly predation on eggs.

Bait Shyness and FAL

FAL is the behavior that presumably underlies bait shyness. Investigations on the relations between FAL and bait shyness continue, particularly with baits containing rodenticides (e.g., Sridhara 1983*a,b*; Bhardwaj et al. 1984; Narendra Kumar 1988; Naheed and Khan 1989*a,b*, 1990; Singh and Saxena 1991). The studies are based on FAL and the generalization of learned avoidance from one stimulus to other similar stimuli (Figure 1).

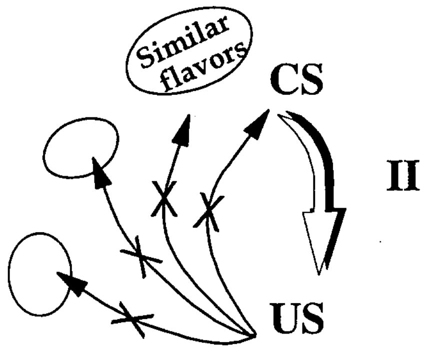

FIGURE 1. The model of flavor aversion learning commonly used in studies of vertebrate pesticides or repellents. Food containing a poison or repellent (CS, conditioned stimulus) is ingested by the animal which, following an interval of time (II. interstimulus interval), suffers a postingestional illness (US, unconditional stimulus). Subsequently, the animal avoids the food and, by generalization of the learned aversion, other foods having similar flavors (or, for birds, visual cues).

For example, Sridhara (1983*b*) studied stimulus generalization of aversions learned from baits containing either zinc phosphide or Vacor (N-3-pyridylmethyl-N1-P-nitrophenylurea) by the Indian gerbil (*Tatera cuvieri*). After a single pairing with a bait containing either rodenticide, gerbils avoided both the cereal and the oil components of the bait as well as novel poisons and nonpoisonous but novel foods. Sridhara (1983*b*) explained the results as involving FAL and illness-enhanced neophobia. Bhardwaj et al. (1984) established that the flavors of zinc phosphide baits containing sugar were more salient (i.e., likely to be associated with illness, Kalat and Rozin 1971) conditioned stimuli than those containing groundnut oils for roof rats (*Rattus rattus*). The rats also failed to generalize learned aversions from flavors of baits containing the oils to those comprised of cereal mixtures. Naheed and Khan (1989*a*) established that bait shyness subsequent to poisoning with barium carbonate by surviving wild *R. rattus* could be reduced or eliminated by changing such stimuli as the texture of the cereal baits, the bait flavor by adding chocolate, or by changing the proportions of cereal to groundnut oil in the bait. Naheed and Khan used similar experimental designs to study aversions learned by *R. rattus* to arrays of baits containing the rodenticides ANTU (alpha-napthylthiourea, 1989*b*) and thallous sulphate (1990). With ANTU, rats subsequently avoided baits containing the poison. Avoidance was generalized to some, but not all (such as "oily") untreated baits. With thallous sulphate, rats learned to avoid the baits. However, if the concentration of thallous sulphate was kept at or below 8 mg/10 g of bait, the rats accepted different flavored baits containing the poison. Singh and Saxena (1991) found that *R. rattus* learned aversions to baits containing zinc phosphide. FAL persisted for 45 or more days, and was prolonged by repeated exposures to baits containing the poisons.

FAL has also been used to infer the taste qualities of rodenticides for Norway rats (*R. norvegicus*) by assessing the extent of generalization of learned aversions to other materials representing an array of flavors. Following methodology established by Stewart et al. (1983), Mason et al. (1985) found that avoidance learned by *R. norvegicus* to the flavor of strychnine generalized to other flavors that taste bitter to humans. By mixing different bitters in proportion to the degree of generalized avoidance, Mason et al. (1985) developed a nontoxic flavor "mimic" of strychnine. Using the same experimental approach, Mason et al. (1991) inferred that scilliroside (the active ingredient in red squill) was essentially tasteless to *R. norvegicus*, whereas alpha-chlorohydrin and ANTU tasted "bitter" and "sour," and calciferol tasted "bitter" and "sweet." Aversions learned to sodium warfarin generalized to "bitter," "sweet," and "salty" flavors. From these two series of studies, the investigators concluded that FAL could be used to help to develop prebaits and bait enhancers, and to empirically evaluate the effectiveness of microencapsulation techniques.

Registration or Reregistration of Existing FAL-Based Pesticides

Registration refers to a regulatory determination by the U.S. Environmental Protection Agency (EPA) that the benefits from using a potential new repellent, or a pesticide already registered in a different way, outweigh the environmental risks. Reregistration refers to a 1988 Amendment to the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) of 1947 in which all pesticides containing an active ingredient registered before November 1984 must be reregistered within 9 years (i.e., by 1997). Both registration and reregistration are based on evaluations of scientific information on product chemistry, toxicity to nontarget organisms, human health hazards, environmental fate, and environmental residues. All data must be provided according to guidelines established by Good Laboratory Practice Standards. Data requirements are particularly rigorous for repellents applied for food uses, such as on crops. An evaluation of the recent economic impacts on research in vertebrate pesticides within the United States was provided by Fagerstone et al. (1990).

Prior to the 1988 Amendment to FIFRA, Mesurol (methiocarb: (3,5–dimethyl–4–methylthiophenol methylcarbarmate) was the only compound registered for use as an avian repellent in the United States for which its mode of action was FAL (Rogers 1974, 1978*b*). Research centered on both new or more effective uses and, after 1988, also on reregistration.

New uses included evaluations of methiocarb as an unconditioned stimulus for learned aversions by rodents such as meadow voles (*Microtus pennsylvanicus)* (Swihart 1990) and deer mice (*Peromyscus maniculatus)* (Holm et al. 1988). New uses also included the evaluation of effectiveness on additional bird species and situations, such as protecting orchids and anthuriums from red-vented bulbuls (*Pycnonotus cafer*) and Japanese white-eyes *(Zosterops japonicus)* (Cummings et al. 1994); avoidance of shelled corn by captive Canada geese (*Branta canadensis*) and mallards (*Anas platyrhynchos)* (Cummings et al. 1992); and, species of birds (*Columba livia, Lonchura striata, Passer domesticus,* and *Psittacula krameri*) that commonly cause damage to crops in Bangladesh (Sultana et al. 1986).

One approach for making methiocarb a more effective bird repellent for granivorous birds was to add visual or flavor cues that could become highly salient conditioned stimuli. Mason and Reidinger (1983*b*) found that adding novel and distinctive visual cues improved the efficacy of methiocarb in laboratory trials and suggested that visual cues such as flags might be tried in field tests. In a separate series of studies with red-winged blackbirds (*Agelaius phoeniceus*) and using methiocarb as the unconditioned stimulus, Mason and Reidinger (1983*a*) found that quality and shades of color influenced the effects of preexposure as well as the extent of generalization of color enhanced FAL. In a third series of trials, Mason and Reidinger (1983*c*) showed that flavor and color could be variously important as cues for FAL for European starlings (*Sturnus vulgaris*), depending on the context in which the cues occurred. They suggested that generalization of learned aversions might be one useful criterion for selecting colors for enhancing bird repellents.

Concomitant with these studies, Bullard et al. (1983) conducted both laboratory and field trials in Africa and the Philippines to assess whether wattle tannins added to a methiocarb solution enhanced the repellent effects with the African weaver finch *Quelea quelea*), the European tree sparrow *Passer montanus*), and the nutmeg mannikin *Lonchura punctulata*). The formulations were sprayed directly on ripening sorghum, millet, and wheat at varying concentrations of methiocarb. Not surprisingly, Bullard et al. (1983) found that the flavor and visual cues of methiocarb alone were insufficient for FAL. Methiocarb repellency was enhanced by the addition of wattle tanin. Elmahdi et al. (1985) found that methiocarb repelled the African weaver finch more effectively with the addition of calcium carbonate as a white coloring agent on wheat, rice, white sorghum, and red sorghum. Calcium carbonate did not enhance the repellency of methiocarb when tested in sorghum plots with blackbirds at the Ottawa National Wildlife Refuge. Dolbeer et al. (1992) speculated that failure of calcium carbonate to enhance repellency over methiocarb-only plots might have been because methiocarb-only treatments also left white spots on the leaves, serving as a comparable form of visual enhancement to calcium carbonate.

Mason (1989) suggested that aposematic (i.e., signaling aversive consequences) colors, such as orange or red for red-winged blackbirds, might be more effective than white in enhancing the repellent effects of methiocarb. Although he did not test the colors, Mason (1989) did compare white (i.e., calcium carbonate) with methyl anthranilate (a trigeminal irritant) in laboratory trials, and found the latter more effective in enhancing the repellent effects of methiocarb with apples. An aposematic odor, pyrazine (2-methoxy-3-methylpyrazine), following pairing with methiocarb, reduced rice consumption by red-winged blackbirds in enclosure trials, and the effect continued after pyrazine was no longer present (Avery and Nelms 1990). Red dye interfered with the effect. These findings may be partly explained by the potentiation of olfactory (e.g., Rusiniak et al. 1979) or visual cues (e.g., Brett et al. 1976; Clarke et al. 1979) that occurs when such cues are paired with a flavor-conditioned stimulus in FAL (e.g., Garcia 1981).

Another approach making methiocarb a more effective bird repellent was to reduce the portion of crop that needed to be treated to protect the whole crop, thereby reducing overall application costs. A conceptual basis for the approach was Batesian mimicry (Mason and Reidinger 1983*b*, Reidinger and Mason 1983, Conover 1984, Avery 1985, Tobin 1985) wherein a bird that learns to avoid visual or other cues associated with the methiocarb-treated portion of a crop (i.e., the "model") would generalize the aversion to the similar appearing, but untreated, portion of the crop (i.e., the "mimic") and also avoid it. Aviary trials treating only portions of crops with methiocarb were effective in reducing damage by brown-headed cowbirds (*Molothrus ater*) and red-winged blackbirds (Avery 1989). In one field evaluation, Tobin et al. (1989) treated every other row of cherry trees with methiocarb. Treated plots had significantly less bird damage than control plots. Although effective, the treatment was not economical, saving an estimated $0.80 in bird damage for every $1.00 spent on application and chemical costs.

As part of the requirements for reregistration, Dolbeer et al. (1994) completed a review of studies on hazards of methiocarb as a bird repellent in fruit crops in lieu of replicated field trials. The review included 33 field studies in 28 locations. The authors concluded from the evaluation that treated plantings averaged 15% loss of fruit compared with 36% for nearby untreated plantings. Methiocarb, applied at 1.7 kg a.i./ha, did not adversely affect birds. In recent studies, scientists have also attempted to reduce application rates on fruit such as blueberries to bring residues within tolerances established by the EPA (e.g., Avery et al. 1993*b*).

In spite of these efforts, I know of no compounds that are registered for use in the United States for use specifically as bird repellents and for which the mode of action is FAL.

Use of Registered Pesticides as FAL-Based Vertebrate Repellents

In attempts to develop effective bird repellents that are also affordable to register, some scientists have focussed on compounds already registered with the EPA as other pesticides (e.g., fungicides, insecticides, or molluscicides), and assessed whether these compounds might also coincidentally function as effective vertebrate repellents. Such compounds might be registered for the new use without duplicating many of the registration requirements, thereby reducing overall costs. The mode of action, also coincidental, may or may not involve FAL.

Trimethacarb (2,3,5-trimethylphenyl methylcarbonate) is an insecticidal carbamate mixture with toxicological characteristics similar to methiocarb. The compound was tested by Nicolaus et al. (1983) for effectiveness in inducing FAL to eggs in crows (*Corvus brachyrhynchos*). Bruggers et al. (1984) considered it as a potential bird repellent on broadcast seed and ripening crops in Haiti, India, Philippines, Bangladesh, Mali, and the United States. It affected germination of sorghum, but not rice and millet seeds. Degradation was rapid when applied at 4 kg a.i./ha. Bruggers et al. (1984) concluded that trimethacarb warranted further evaluation as a bird repellent for crops. Because trimethacarb was being registered in a granular formulation as an insecticide for use on turf, Avery et al. (1989) tested the effectiveness of the formulation as a repellent to deter grazing by American coots (*Fulica americana*). In aviary trials, they found that grazing activity was reduced for about 3 days. Addition of methylpyrazine, a strong odorant, enhanced the effect, but rain and a change in coot grazing behavior prevented an extensive evaluation of the effectiveness of the approach. In a field trial of methiocarb as a potential mouse repellent for no-till plantings, the compound appeared ineffective in reducing mouse damage (Matschke et al. 1988).

Phosmet is registered as Imidan, an insecticide used on blueberries and cherries. Avery et al. (1994*c*) recently evaluated phosmet for its potential as a bird repellent for these crops. At concentrations that varied with species, and in two-cup feeding trials, food containing phosmet was avoided by all three species tested (cedar waxwings [*Bombycilla cedrorum*], American robins [*Turdus migratorius*], and European starlings). They concluded that phosmet might protect small fruit crops from damage by birds. Whether FAL was actually involved in the avoidance was not determined.

Imidacloprid (1-((6-chloro-3-pyridinyl)methyl)-4,5-dihydro-N-nitro-1-H-imidazol-2-amine), is an insecticide being registered as a seed treatment for rice, cotton, wheat, and other crops. Avery et al. (1993*c*, 1994*a*) evaluated its effectiveness in cage and pen trials as a bird repellent using male red-winged blackbirds and brown-headed cowbirds, dyed and undyed rice seeds, and undyed wheat seeds. They concluded that the compound effectively repelled the birds with minimal avian hazard. Avery et al. (1993*c*) suggested the mode of action involved FAL because the bird exhibited no distress or irritation when first eating the treated seeds.

Kocide SD is a copper-based fungicide registered for use on rice seed. Avery and Decker (1991) and Avery et al. (1994*b*) have conducted aviary and field trials to evaluate the effectiveness of Kocide SD as a bird repellent at the concentrations registered for use on rice seed. They found the effectiveness was more pronounced (33% versus 2% average rice seed loss, untreated versus treated plots) in the aviary than in field trials. Nonetheless, Avery et al. (1994*b*) concluded the treatment was cost-effective as a bird repellent and provided protection against fungal pests. The mode of action is unknown, but the compound appears to have a physiological effect on the birds.

DRC–156 is a pesticide being registered for use on golf courses. The formulation is proprietary. It has been tested by Denver Wildlife Research Center scientists for its effectiveness as a Canada goose repellent on turf, and DRC–156 appears to function by FAL. Cummings (1993) reported effective repellency of the compound with geese for over 40 days following a single application.

Fewer efforts have been made to find existing pesticides that repel mammals. Thiram (tetrathylthiuram disulfide) is used as a foliar spray to reduce damage by snowshoe hares (*Lepus americanus*) to forest seedlings. Campbell and Evans (1989) found it reduced damage to Douglas-fir seedlings by mountain beavers *(Aplodontia rufa)*. Thiram is believed to serve as an unconditioned stimulus for FAL. Its effectiveness as a long-term deterrent for forest seedlings has been questioned by Rangen et al. (1993). Laboratory studies have also been conducted on the use of insecticides as unconditioned stimuli for FAL with rodents. Swihart and Conover (1991) found the insecticides Cygon and Sevin to be ineffective in reducing consumption of Romaine lettuce by woodchucks (*Marmota monax*). Alachlor, dinoseb, and fluchoralin produced learned aversions to saccharin solutions in mice when administered both orally and dermally (Mitchell et al. 1989). Maneb produced a learned aversion in the mice when administered orally, but not dermally (Mitchell et al. 1989). The organophosphates dichlorvos, parathion, and diisopropylflurophosphate produced learned aversions in Sprague-Dawley rats (Roney et al. 1986), but possible field applications have not been explored.

Use of Naturally Occurring Substances as FAL-based Vertebrate Pesticides

Naturally occurring substances, particularly those generally regarded as safe or common, have been tested by scientists in pursuit of an affordable vertebrate repellent. In his summary article on natural products that repel or attract wildlife, Bullard (1985) stated that the steam distillate of wild ginger (*Asarum caudatum*) was repellent to deer, elk, hare, rats, and birds. He indicated that foxglove (*Digitalis purpurea*) was repellent to elk and hares, and that a sesquiterpene lactone called Glaucolide A was repellent to cottontail rabbits and white-tailed deer. Nolte et al. (1995) found that a simple water extract of digitalis (*Digitalis purpurea*) reduced consumption of apples by mountain beaver.

Crocker and Perry (1990) evaluated twelve compounds, nine belonging to the cinnamic acid family, for their repellent effects on quail (*Coturnix coturnix*). They were unable to obtain clear evidence of whether repellency was the consequence of FAL or primary aversion, but determined that cinnamide effectively reduced pellet consumption by the birds. Cinnamide and 3,5 dimethylcinnamic acid were both effective repellents with rock doves (*Columba livia*). Avery and Decker (1992) recently evaluated cinnamic acid esters, volatile chemicals in doveweed (*Eremocarpus setigerus*), that are avoided by deer and mourning doves. One of the esters, methyl cinnamate, prevented birds from eating rice. Because the repellent effects were immediate, Avery and Decker (1992) suggested that FAL was not the primary mode of action, but rather trigeminal stimulation.

Jakubas and Gullion (1991) found that naturally occurring coniferyl benzoate deterred feeding of quaking aspen by ruffed grouse. Jakubas et al. (1992) felt that at least part of the effect was due to postingestional malaise and FAL. In that study, benzoate esters appeared more repellent to European starlings than their corresponding alcohols. The scientists felt that crops might be genetically engineered to produce analogs of coniferyl alcohol as a natural defense against birds and other pests.

D-pulegone is used as a naturally occurring mint flavorant for human foods, but has both insecticidal and vertebrate repellent properties (Mason 1990). In his laboratory trials evaluating the repellent properties of d-pulegone with European starlings, Mason (1990) indicated the repellent appeared primarily trigeminal, but that the compound is a reversible cholinesterase inhibitor and may also serve as an unconditioned stimulus in FAL.

Martinez del Rio et al. (1988) and Martinez del Rio (1990) reported that red-winged blackbirds, common grackles (*Quiscalus quiscula*), and European starlings showed differential responses in their preferences for glucose and fructose solutions. Grackles, with higher sucrase activity, preferred sucrose, whereas starlings, lacking sucrase, rejected concentrated solutions of sucrose. Martinez del Rio et al. (1988) suggested that the insectivorous nature of starlings that resulted in their inability to digest sucrose, and Martinez del Rio (1990) provided further evidence that sucrase activity can have significant behavioral and ecological consequences.

Brugger and Nelms (1991) explored the possibility that lack of sucrase in the digestive system of the American robin might, on consumption of sucrose, lead to postingestional illness and FAL. Brugger (1992) suggested that a fruit cultivar would require as much as 15% sucrose to repel robins, and would require extensive replacement of simple sugars by sucrose, which might be possible through breeding. Brugger et al. (1993) suggested that such fruit cultivars would require at least 11.25% sucrose to repel starlings. Darnell et al. (1994) examined the variability in sucrose levels in wild and domestic blueberries (*Vaccinium spp.*). They found a threefold difference in sucrose concentrations among varieties, with sucrose occurring in the fruits at ripening. They concluded both the patterns of sucrose accumulation and its variability in concentration among species support the feasibility of developing fruits with high sucrose content, which could help to minimize losses to some bird species. Clark and Mason (1993) compared avoidance of sucrose by European starlings with that of methyl anthranilate. They concluded that sucrose alone is not sufficiently aversive to repel bird pests in field settings.

Mason and Clark (1994) tested the notion that naturally occurring substances like activated charcoal and quartz sand might induce FAL by their abrasive actions on the gut of European starlings. Both compounds reduced feeding on chow, without evidence of lesions in the gut. They suggested activated charcoal added to cattle feed might be useful as a bird repellent and that quartz sand might be useful as a repellent additive to landfill covers.

Use of FAL to Reduce Predation on Eggs and Wildlife

In 1983, Nicolaus et al. demonstrated that free-ranging crows avoided distinctively colored eggs following ingestion of ones treated with illness-inducing trimethacarb and FAL. Concomitant with Mason and Reidinger (1983*b*), they suggested that Batesian mimicry might serve as a basis for crop or prey protection wherein predators learn to avoid prey through ingestion of treated prey and FAL (i.e., "models") and through generalization of the learned aversions to other similar, but untreated, prey (i.e., "mimics").

Nicolaus (1987) injected surrogate sandhill crane eggs (*Grus canadensis*) with trimethacarb to determine if FAL might protect some of the eggs from predators. Depending on the experimental manipulations, eggs were dyed or not dyed, and dyed eggs were treated with trimethacarb or not treated. Predators were mostly common ravens (*Corvus corax*), but included also magpies (*Pica pica*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), long-tailed weasels (*Mustela frenata*), and badgers (*Taxidea taxus*). Nicolaus (1987) reported reduced consumption and attacks on surrogate eggs in treatment sites compared to control sites. Avoidance continued through fluctuations in availability of alternate foods, and critical reproductive periods. He concluded FAL could be an important factor in the evolution of aposematism and mimicry and that these concepts might be applied to protect the eggs of more desirable or endangered species.

In subsequent studies, Nicolaus et al. (1989*a,c*) explored the use of oral estrogen, ethinyl estradiol, as an unconditioned stimulus for FAL. The estrogens were injected into eggs and appeared undetected by predators that fed on the eggs. Nicolaus et al. (1989*a*) also found a dose dependent effect on strength of aversions in male and female rats. Nicolaus et al. (1989*c*) demonstrated that predators avoided both treated (i.e., "model") and untreated (i.e.,"mimic") eggs. Nicolaus et al. (1992) examined longevity of estrogen in egg baits and found that the baits induce aversions in female rats for up to 8 days in egg albumen and up to 4 days in egg yolk, both at room temperature. Miele et al. (1988) demonstrated that estradiol benzoate, but not progesterone or testosterone propionate, could cause postingestional illness that served as a potent unconditioned stimulus in FAL in male and female mice (*Mus musculus*).

Nicolaus et al. (1989*b*) investigated the use of another illness-inducing substance, carbachol (carbamylcholine chloride), with both captive ravens and free-ranging crows. They found that captive ravens learned to avoid favored food under conditions of chronic and sometime acute food deprivation. Free-ranging crows, after consuming chicken eggs with 18 mg of carbachol, subsequently avoided untreated eggs that looked both similar and dissimilar to the treated ones. Nicolaus et al. (1989*b*) felt that carbachol had advantage over other illness-inducing substances because it was water soluble, and therefore could be mixed more uniformly in the eggs.

Dimmick and Nicolaus (1990), using sweet-green chicken eggs and breeding pairs of crows at sites in Illinois and Iowa, varied percentages of eggs containing trimethacarb at 0%, 12.5%, 50%, and 100%. The crows learned to avoid colored eggs at all treated sites, and they abandoned sites at the lower treatment levels. In a followup study a year later, crows had returned to all sites, but they continued to avoid eggs at sites where 50% of the eggs had been treated. Dimmick and Nicolaus (1990) concluded that placement should contain an adequate, but not necessarily large, number of illness-inducing baits for an effective control program.

In 1987, Nicolaus and Nellis tested the effectiveness of eggs treated with carbachol in reducing predation by mongoose on endangered marine turtle eggs in the U.S. Virgin Islands. They found suppression of egg consumption among treated eggs was 37% when compared with controls, but that olfactory cues were ineffective in eliciting avoidance from a distance. Most recently, Semel and Nicolaus (1992) tested the effectiveness of estrogen-treated eggs in reducing predation by free-ranging raccoons.

Avery and Decker (1993) found that methyl anthranilate, either alone or in combination with injections of methiocarb at 18 mg/egg, effectively reduced consumption of quail eggs (*Coturnix japonica*) by captive fish crows (*Corvus ossifragus*). They noted that some birds were persistent in their attempts to consume the eggs. Avery et al. (1993*a*) placed quail eggs injected with 30 mg of methiocarb at three nesting colonies of the California least tern (*Sterna antillarum browni*) and at four simulated colonies at the U.S. Marine Corps Base, Camp Pendleton, CA. The treated eggs were taken by common ravens at each nesting colony and at three of four simulated colonies. No tern eggs were lost at the nesting colonies, and no ravens were killed to prevent such predation. In fact, nesting ravens near the colonies defended their territories against other ravens, serving as a biological buffer zone that further protected the least tern eggs from predation. Avery et al. (1993*a*) recommended a strategy wherein surrogate eggs treated with methiocarb were used first to train ravens to avoid least tern eggs and that ravens be killed only if FAL was unsuccessful.

DISCUSSION

I summarized the recent literature in FAL related to wildlife damage management and illustrated four research directions. Firstly, strategies that reduce registration or reregistration costs have become a dominant research consideration for some scientists between 1983 and the present. One can hardly argue against the need to consider, at the earliest stages of any directed research activity, the likelihood that successful research outcomes will lead to actual applications. Expenses involved with registration of repellents, even ones with nontoxic modes of action, can make the difference between eventual profit or loss and, therefore, use of the repellent.

Nonetheless, limiting the evaluation of potential new vertebrate repellents to compounds that have already been registered for use as fungicides, insecticides, or molluscicides, or to common or naturally occurring and commonly regarded as safe materials, seems to me to be too constraining. To the extent that any new research is a risk, and scientists are gamblers, I believe that the odds are more geometric than additive for finding a compound whose chemical attributes make it particularly effective as an illness-inducing agent for vertebrate FAL and that also serves as an effective fungicide, insecticide, molluscicide, or other type of pesticide.

Another approach is to evaluate the stereochemical relationships between groups of chemicals that are effective unconditioned stimuli for FAL in vertebrates, and develop chemical models for such stimuli. Were such a systematic approach successful so that it led to identification of the chemical characteristics of effective vertebrate illness-inducing agents, registration and other criteria might then be applied in the selection of actual compounds for bioassay and field tests. An analogous approach has already been applied successfully in the development of primary bird repellents (e.g., see Clark, "A review of the bird repellent effects of 117 carbocyclic compounds," this symposium proceedings).

Secondly, few efforts have been made to use FAL as a research tool in the development of vertebrate repellents. Reidinger and Mason (1983) summarized uses of FAL and its attributes as they might apply to the development of rodent and bird control, including the development of prebaits, bait attractants or repellents, bait enhancers, and masking agents, and for the development of baiting combinations to avoid bait shyness. Limited work with these types of applications has been summarized herein (Sridhara 1983*b*; Stewart et al. 1983; Bhardwaj et al. 1984; Naheed and Khan 1989*a,b*, 1990; Mason et al. 1991), but potential useful applications have only begun to the whole area of repellent research for vertebrates.

Some research has focused on semiochemicals as primary repellents for vertebrates, such as the elucidation of predator flavorants and deodorants avoided by prey (e.g., Epple et al. 1993) or the presence of compounds that signal successful foraging (e.g., Bean et al. 1988). Perhaps FAL and generalization to similar tastes or odors could be used to infer actual flavors or odors of these compounds to vertebrates of interest. In turn, that information might be used to develop repellent models or empirically derived synthetic substitutes.

In some instances, more attention might have been paid to FAL and its attributes in the design and interpretation of results. For example, Avery et al. (1994*a*) used two-choice preference tests to evaluate the effectiveness of imidacloprid as a repellent with captive red-winged blackbirds. Treated and untreated rice or wheat were placed in cups, and the cups were assigned at random to either a left or right location in a cage. A similar procedure was followed in assessing the effectiveness of imidacloprid as a repellent for brown-headed cowbirds. Repellency was assessed by measuring the amount of untreated versus treated food that was consumed. Although the approach documented reduced consumption of the treated over untreated foods, the design may have been confounded by generalization of aversions learned from the treated to untreated foods. This might help to explain significantly reduced consumption of both treated and untreated rice by cowbirds during the first 3 days (mean of 1.8 g/bird compared to a mean of 2.3 g/bird on days 4 and 5) after exposure to treated baits. Perhaps a distinctive color cue in a counterbalanced design would help the birds differentiate between treated and untreated baits. Appropriate color combinations could be assessed through FAL and generalization tests.

Thirdly, all of the studies reported were based on a single model of FAL (Figure 1). Repellent systems based on the model include several assumptions. One is that the repelled animals will infrequently resample the food or prey; another is that the predator will not learn fine flavor or visual discriminations. In many field situations, these assumptions could be problematic.

Other models, based on FAL, exist that do not depend on these assumptions. One (Reidinger and Mason 1983) takes advantage of salience and oveshadowing. Although Kalat and Rozin (1971) defined salience as the likelihood of being associated with illness, Kalat (1974) further described salience as dependent on novelty (i.e., divergence from adaptation level) rather than concentration per se in FAL. The importance of novelty in salience has since been supported by other studies (e.g., Provenza et al. 1993, 1995). When presented with confounded flavor stimuli, animals learn to avoid the more salient one, and associations with the less salient stimuli are blocked (i.e., overshadowing, Kalat and Rozin 1973). If they have adequate diets, animals learn aversions to the more salient flavor in situations where they are exposed to several flavor stimuli in a confounded fashion followed by a postingestional illness (Figure 2).

Suppose that one uses a nonsalient, nontraditional bait (e.g., an isotonic LiCl solution) placed near a crop so that a rodent were likely to sample both the bait and the crop in a confounded manner. Presumably, the rodent would receive a postingestional illness and learn an aversion to the more salient stimulus, the crop. In subsequent foragings, the experience would be repeated (along with other combinations), and the aversion would probably be reinforced. When the flavor of the crop changed (e.g., when rice reached flowering or milky-dough stage, or a pesticide was applied), the rodent would learn a new aversion, again to the crop. Such a model assumes that the pest will sample the crop or prey even after learning an aversion. It also assumes the pest will make even fine visual or flavor discriminations. Because the bait is not applied directly to the crop, it would need less data to meet the EPA's registration requirements.

Although not conducted in the context of wildlife damage management, a study by Burritt and Provenza (1989) support this notion. Burritt and Provenza (1989) determined whether lambs

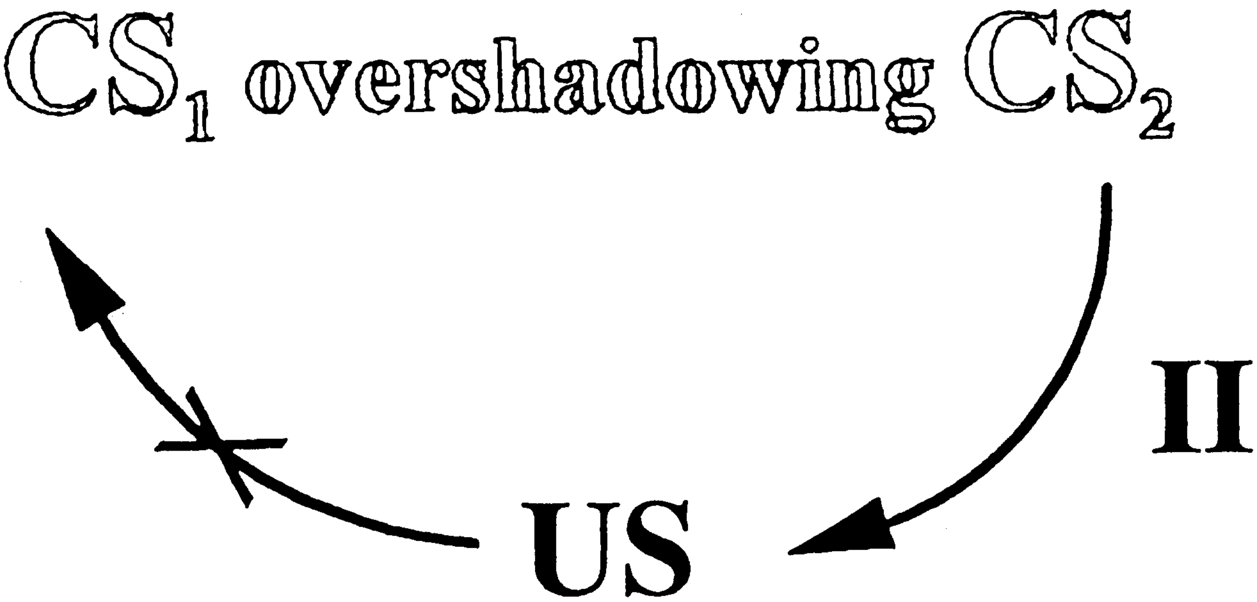

FIGURE 2. A model of flavor aversion learning involving salience (i.e., likelihood of being associated with illness) and overshadowing (i.e., when presented confounded stimuli, the animal learns to avoid the moss salient one) rather than generalization. The animal ingests two different tasbing (or, for binds, different appearing) foods (CS_1 and Cm_2) in a crnfounded manners the least salient of which (i.e., CS_2) contains a poison. Subsequently, the animal avoids CS_1.

would avoid a novel food (milo) even though the toxin lithium chloride (LiCl) was administered to them through a familiar food (barley). Lambs first received barley treated with sodium chloride (NaCl) for 3 weeks. In daily trials following the barley–NaCl exposure, lambs first received milo and then received barley treated with LiCl. Lambs stopped consuming milo but did not reduce barley consumption, even though the barley contained the LiCl. Thus, the lambs either did not detect or did not respond to the differences between the LiCl- and NaCl-treated barley, and they clearly avoided the food (milo) that was most novel.

Other paradigms involving FAL might also be conceived and tested (e.g., Mason and Reidinger 1983*c*).

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FIGURE 2. A model of flavor aversion learning involving salience (i.e., likelihood of being associated with illness) and overshadowing (i.e., when presented confounded stimuli, the animal learns to avoid the most salient one) rather than generalization. The animal ingests two different tasting (or, for birds, different appearing) foods (CS_1 and Cm_2) in a confounded manner the least salient of which (i.e., CS_2) contains a poison. Subsequently, the animal avoids CS_1.

SUMMARY

I illustrated four directions in present research on FAL as it relates to wildlife damage management: (1) continued applications of FAL to improved understanding of bait shyness, particularly as it relates to rodenticides; (2) continued studies for the registration or reregistration of vertebrate repellents that act via FAL; (3) evaluation of pesticides already registered for other uses, or naturally or commonly occurring substances, for the repellent effects on vertebrates; and (4) application of FAL in a Batesian mimicry model to protect food or desirable prey from predators, particularly eggs of endangered species. The studies have focused on a single model of FAL in which the vertebrate pest ingests a food or other substance, suffers a postingestional consequence, learns to avoid the food or similar objects, and subsequently avoids them (i.e., repellency).

Some research strategies are driven by concerns for costs of registration or reregistration of putative repellents that might emerge from the research. Consequently, the range of potential repellents being considered is restricted. There are no pesticides presently registered specifically as vertebrate repellents whose modes of action are known to be through FAL. Nonetheless, FAL remains an important concept whose potential contributions to the development of vertebrate repellents have not been fully exploited. FAL might be used to infer flavors or other signals of repellents, to improve baits and baiting systems, and to improve or help to explain results from repellency tests. Other models of FAL involving saliency and overshadowing should be considered in the development of vertebrate repellents.

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